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Published in:
Science Magazine

DOI:
10.1126/science.aas9411

Publication date:
2018

DOMESTICATION

Ancient goat genomes reveal mosaic domestication in the Fertile Crescent

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Current genetic data are equivocal as to whether goat domestication occurred multiple times or was a singular process. We generated genomic data from 83 ancient goats (51 with genome-wide coverage) from Paleolithic to Medieval contexts throughout the Near East. Our findings demonstrate that multiple divergent ancient wild goat sources were domesticated in a dispersed process that resulted in genetically and geographically distinct Neolithic goat populations, echoing contemporaneous human divergence across the region. These early goat populations contributed differently to modern goats in Asia, Africa, and Europe. We also detect early selection for pigmentation, stature, reproduction, milking, and response to dietary change, providing 8000-year-old evidence for human agency in molding genome variation within a partner species.

The Fertile Crescent of Southwest Asia and adjacent areas were the location of transformative prehistoric innovations including the domestication of sheep, goats, cattle, and pigs (*1*–*3*). Archaeological evidence suggests local development of wild goat (bezoar) management strategies in different regions in the mid- to late 11th millennium before the present (BP) with domestic phenotypes emerging in the 10th millennium, first in the Anatolian region (*4*–*6*). A key question is whether these early patterns of exploitation are consistent with a geographically focused singular domestication process or whether domestic goats were recruited from separate populations, with parallel genetic consequences. Genetic evidence is inconclusive (*7*, *8*).

We generated ancient *Capra* genome data from Neolithic sites from western (Anatolia and the Balkans), eastern (Iran and Turkmenistan), and southern (Jordan and Israel) regions around the Fertile Crescent (tables S1 to S3). To maximize yields, we sampled mainly petrous bones; 51 such samples produced nuclear genome coverage ranging from 0.01× to 14.89× (median 1.05×) (tables S4 and S5). We enriched for mitochondrial DNA (mtDNA) in poorly preserved samples and obtained a total of 83 whole mitochondrial genomes (median 70.95×) (table S6 and figs. S1 and S2) (*9*).

The majority of our ancient domestic mitochondrial sequences fall within modern haplogroups A, B, C, D, and G (Fig. 1A, figs. S3 to S6, and tables S7 to S9). The Paleolithic wild goat samples fall exclusively in more divergent clades T [similar to the related wild caprid, the West Caucasian tur (*Capra caucasica*)] and F [previously reported in bezoar and a small number of Sicilian goats (*10*)]. Here, we found F in a >47,000 BP bezoar from Hovk-1 cave, Armenia; in a pre-domestic goat from Direkli Cave, Turkey; and in Levantine goats at 'Ain Ghazal, an early Neolithic village in Jordan, and Abu Ghosh, Israel.

A geographic plot of Neolithic samples illustrates that early domestic goat haplogroups are highly structured (Fig. 1B), with disjunct distributions in the western, eastern, and southern (Levantine) regions of the Near East (tables S10 and S11). In this early farming period, partitioning is significant; analysis of molecular variance (*9*) estimates that 81% of the mtDNA diversity stems from differences between the three regions (P = 0.028, permutation test) (tables S12 and S13). When we use an approximate Bayesian computation (ABC) framework on this mtDNA variation to investigate demographic history, a model suggesting a pre-domestic branching of the divergent Levant population (38,500 to 195,200 BP) is favored. This suggests multiple wild origins of Neolithic goat herds (tables S14 to S19) (*9*). In the later post-Neolithic samples,

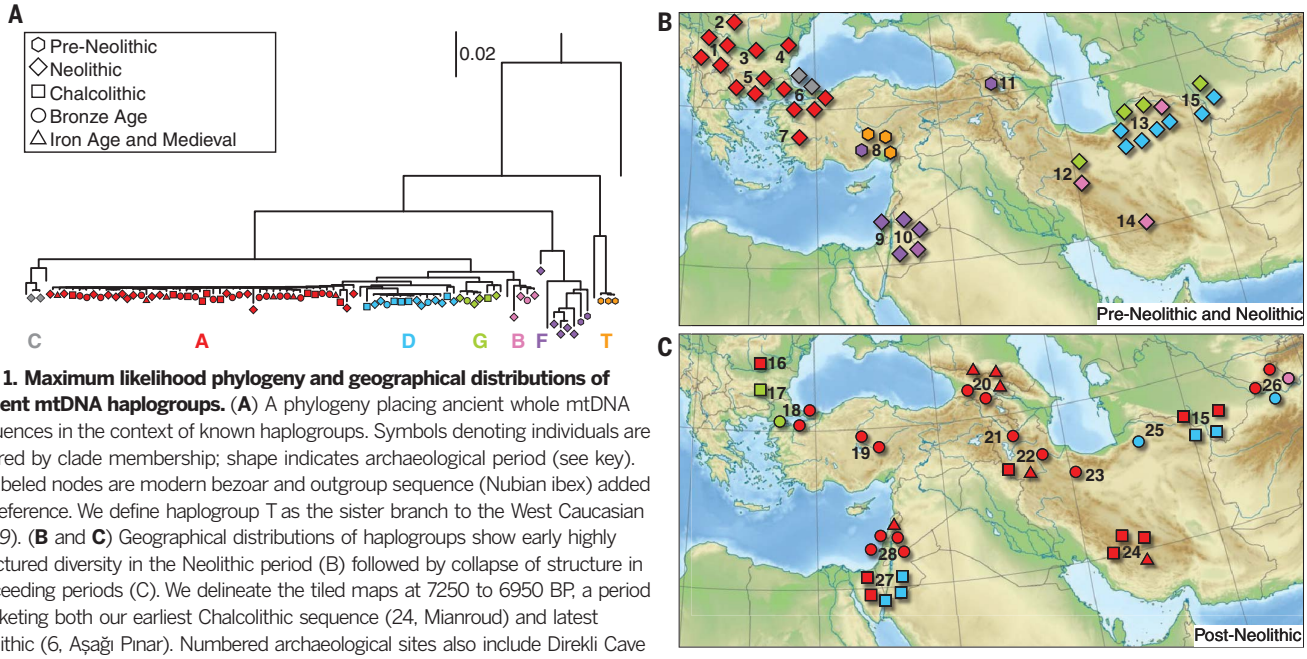

Fig. 1. Maximum likelihood phylogeny and geographical distributions of ancient mtDNA haplogroups. (**A**) A phylogeny placing ancient whole mtDNA sequences in the context of known haplogroups. Symbols denoting individuals are colored by clade membership; shape indicates archaeological period (see key). Unlabeled nodes are modern bezoar and outgroup sequence (Nubian ibex) added for reference. We define haplogroup T as the sister branch to the West Caucasian tur (*9*). (**B** and **C**) Geographical distributions of haplogroups show early highly structured diversity in the Neolithic period (B) followed by collapse of structure in succeeding periods (C). We delineate the tiled maps at 7250 to 6950 BP, a period bracketing both our earliest Chalcolithic sequence (24, Mianroud) and latest Neolithic (6, Aşağı Pınar). Numbered archaeological sites also include Direkli Cave (8), Abu Ghosh (9), 'Ain Ghazal (10), and Hovk-1 Cave (11) (table S1) (*9*).

this partitioning collapses to zero (Fig. 1C) and the ubiquitous modern haplogroup, A, becomes widespread.

Analyses of genome-wide variation also argue against a single common origin. Neolithic samples from the west, east, and Levant each cluster separately in principal components analysis (PCA; Fig. 2) and in phylogenetic reconstruction (figs. S7 to S10). *D* statistics show that these clusters have significantly different levels of allele sharing with two regional samples of pre-domestic wild goats: a ~13,000 BP population from Direkli cave (Southeast Anatolia) and a >47,000 BP bezoar from Hovk-1 cave (Armenia) (Fig. 3A) (*9*). These differences are consistent with qpGraph estimation of relationships (Fig. 3B, fig. S11, and table S20) where a primary ancestral divide between western and eastern genomes occurred more than 47,000 BP. The latter clade gave rise to the eastern Neolithic population. However, the western and Levant Neolithic goat derive ~50% and ~70% of their ancestry from a divergent source in the western clade that had affinity to the Anatolian wild population, in line with f_4 ratios and Treemix graphs (fig. S12 and table S21). These different proportions infer substantial local recruitment from different wild populations into early herds in regions proximal to each of the different vertices of the Fertile Crescent. ABC modeling of autosomal variation also rejects a single domestication origin scenario (figs. S13 to S15 and tables S11 and S22 to S25) (*9*).

Thus, our data favor a process of Near Eastern animal domestication that is dispersed in space and time, rather than radiating from a central core (*3*, *11*). This resonates with archaeozoological evidence for disparate early management strategies from early Anatolian, Iranian, and Levantine Neolithic sites (*12*, *13*). Interestingly, our finding of divergent goat genomes within the Neolithic echoes genetic investigation of early farmers. Northwestern Anatolian and Iranian human Neolithic genomes are also divergent (*14*–*16*), which suggests the sharing of techniques rather than large-scale migrations of populations across Southwest Asia in the period of early domestication. Several crop plants also show evidence of parallel domestication processes in the region (*17*).

PCA affinity (Fig. 2), supported by qpGraph and outgroup f_3 analyses, suggests that modern European goats derive from a source close to the western Neolithic; Far Eastern goats derive from early eastern Neolithic domesticates; and African goats have a contribution from the Levant, but in this case with considerable admixture from the other sources (figs. S11, S16, and S17 and tables S26 and 27). The latter may be in part a result of admixture that is discernible in the same analyses extended to ancient genomes within the Fertile Crescent after the Neolithic (figs. S18 and S19 and tables S20, S27, and S31) when the spread of metallurgy and other developments likely resulted in an expansion of inter-regional trade networks and livestock movement.

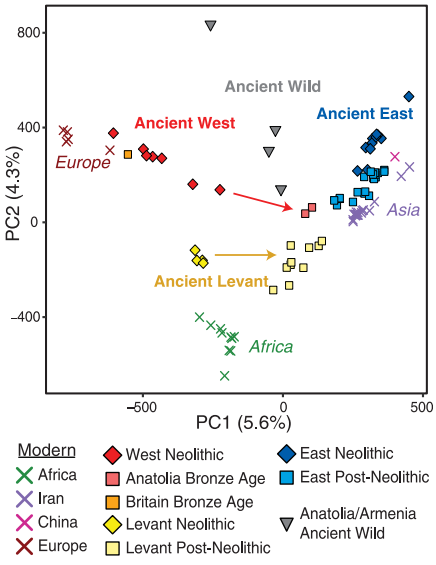

Fig. 2. Principal components analysis of ancient and modern goat genomes. Ancient goats cluster in three vertices: eastern (Iran, Uzbekistan, Turkmenistan, Georgia), western (Balkans, Anatolia), and southern or Levantine (Jordan, Israel) margins of the Near East. Modern European, Asian and, interestingly, African goats follow this pattern, but Bronze Age Anatolian (red arrow) and Chalcolithic/Bronze Age Israeli (yellow arrow) samples show shifts relative to earlier genomes from those regions, suggesting post-Neolithic admixture within the primary regions.

Animal domestication likely involved adaptive pressures due to infection, changes in diet, translocation beyond natural habitat, and human selection (*18*). We thus took an outlier approach to identify loci that underwent selective sweeps in either six eastern Neolithic genomes or four western genome samples (minimum coverage 2×). We compared each population to 16 modern bezoar genomes (*19*) and identified 18 windows with both high divergence (highest 0.1% *Fst* values) and reduced diversity in Neolithic goats (lowest 5% θ ratio: Neolithic/wild; tables S28, S29, and S32).

The pigmentation loci, *KIT* and *KITLG*, are the only shared signals in both Neolithic populations. Both are common signals in modern livestock analyses (*19*, *20*). We thus examined *Fst* values for previously reported coloration genes and identified *ASIP* and *MITF* as also showing high values (Fig. 4, A and B, fig. S20, and table S30). Whereas modern breeds are defined in part by color pattern, the driver of the ~8000-year-old selection observed in the Neolithic for pigmentation may be less obvious. *KIT* is involved in the piebald trait in mammals (*21*) and may have been favored as a means of distinguishing individuals and maintaining ownership within shared herds as well as for aesthetic value. Pigmentation change has also been proposed as a pleiotropic effect of selection for tameness (*22*). Intriguingly, selective sweeps around the *KIT* locus were clearly independent in the eastern and western Neolithic goat sampled genomes, as the resulting locus genotypes are distinct and contribute differently to modern eastern and western populations (Fig. 4C).

Trait mapping in cattle, the most studied ungulate, offers interpretation of three other caprine signals identified here. *SIRT1* (identified in the western Neolithic) has variants affecting stature (*23*), and a reduction in size is a widespread signal of early domestication. *EPGN* (eastern Neolithic) is linked to calving interval; increase in reproductive frequency is another general feature of domestication. *STAT1* (eastern Neolithic) is involved in mammary gland development and has been linked to milk production (*24*). The second most extreme eastern signal maps to a homolog of human *CYP2C19*, which (like other cytochrome P450 products) contributes to metabolism of xenobiotics including enniatin B, a toxic product of fungal strains that contaminate cereals and grains. This selection signal has been hypothesized as a response to early agriculture in humans (*25*). Early recycling of agricultural by-products as animal fodder has been suggested as a motivation for the origins of husbandry (*3*), and fungal toxins may have been a challenge to early domestic goats as well as their agriculturist owners.

Our results imply a domestication process carried out by humans in dispersed, divergent,

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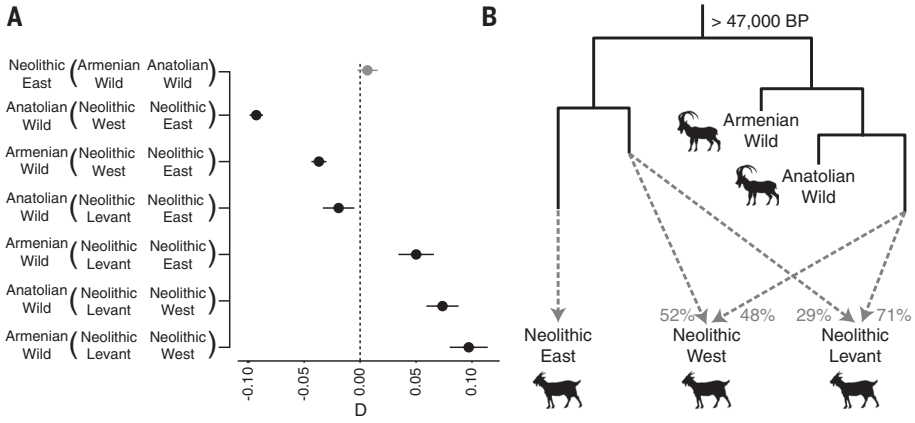

Fig. 3. *D* statistics and admixture graph of ancient and modern goats. (**A**) In the test *X*(*Y*, *Z*), positive or negative *D* values indicate a greater number of derived alleles between *X* and *Z* or *X* and *Y*, respectively; yak is used as an outgroup. *D* values for each test are presented with error bars of 3 SE; a nonsignificant test is shown in gray. These show that regional pre-domestic wild goats relate asymmetrically to Neolithic domestic populations, ruling out a singular origin. (**B**) Admixture graph reconstructing the population history of pre-Neolithic and Neolithic goats. Relative inputs from divergent sources into early domestic herds are represented by gray dashed arrows (drawn from fig. S11F) (*9*).

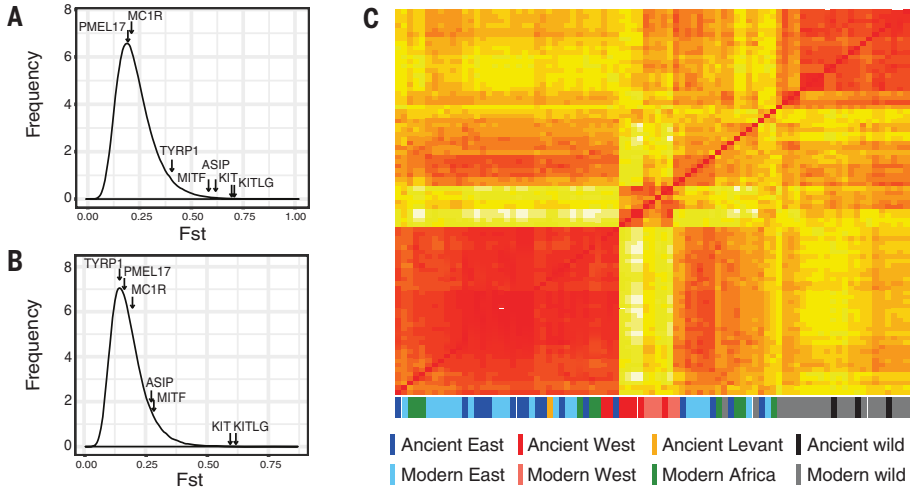

Fig. 4. *Fst* distributions between modern bezoar and Neolithic western and eastern populations, and a heat map of allele sharing between modern and domestic goats at the *KIT* locus. (**A** and **B**) The highest *Fst* values for 50-kb windows overlapping seven pigmentation loci showing evidence of selection in modern goat, sheep, or cattle studies are indicated for western (A) and eastern (B) populations (tables S30 and S32). (**C**) The pigmentation locus, *KIT*, shows evidence of selection in both western and eastern Neolithic samples, but allele sharing distances (illustrated as a heat map) suggest that selection acted on divergent standing variation in parallel but separate processes. Five of the seven ancient western samples are from Neolithic contexts and cluster with modern western haplogroups. The two remaining western ancients (red) falling in the eastern cluster (mainly blue) are Bronze Age Anatolian samples with indications of secondary admixture (Fig. 2).

but communicating communities across the Fertile Crescent who selected animals in early millennia, including for pigmentation, the most visible of domestic traits.

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ACKNOWLEDGMENTS

We thank L. Cassidy, E. Jones, L. Frantz, G. Larson, and M. Zeder for critical reading of the text; the Israel Antiquities Authority for permitting sampling of the Israeli sites (under permit); excavators, archaeozoologists, and museums who permitted sampling from their excavations and collections without which this project would not have been possible, including T. Levy, C. Grigson, A. Maeir, S. Gitin, P. de Miroschedji, S. Davis, and A. Ben-Tor; the Iranian Cultural Heritage Handicraft and Tourism organization and the National Museum of Iran (NMI) and J. Nokandeh, director, and F. Biglari, cultural deputy; H. Laleh and A. Aliyari, Directors of the Archaeometry Laboratory of the University of Tehran. The ATM Project of MNHN supported sampling of several sites as well as the LIA HAOMA CNRS project. We are grateful for assistance from J. Vuković, J. Bulatović, I. Stojanović, H. Greenfield, Wiltshire Museum, L. Brown, and Trinseq. The authors wish to acknowledge the DJEI/DES/SFI/HEA Irish Centre for High-End Computing (ICHEC) for the provision of computational facilities and support. **Funding:** Supported by ERC Investigator grant 295729-CodeX. Additional support from Science Foundation Ireland Award 12/ERC/B2227. P.M.D. was supported by the HERA Joint Research Programme "Uses of the Past" (CitiGen); and the European Union's Horizon 2020 research and innovation program under grant agreement no. 649307. A.M. was supported by ERC Consolidator grant 647787-LocalAdaptation. M.D.T. was supported by the Marie Skłodowska-Curie Individual Fellowship SCRIBE H2020-MSCA-IF-2016 747424. Author contributions: D.G.B. conceived of the project and designed the research, with input from J.B. and M.C.; C.C., R.P., L.M., D.O., B.S.A., N.B., L.K.H., M.M., R.Ke., C.M.E., G.B.O., F.P., T.C., J.D.V., A.F.M., D.D., H.D., Ö.C., R.Kh., H.F., S.B., R.R.S., A.A.V., E.W.S., H.A.K., and S.M. provided samples and data; K.G.D., V.E.M., V.M., A.S., A.J.H., and M.D.T. performed genomics laboratory work; P.M.D. performed ABC analyses, with input from A.M., K.G.D., and D.G.B.; K.G.D. performed the computational analyses with input from D.G.B., V.E.M., M.P.V., and M.D.T.; D.G.B. and K.G.D. wrote the paper, with input from all other co-authors; K.G.D. and P.M.D. wrote the supplementary information, with input from all other authors. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Raw reads and mitochondrial sequences have been deposited at the European Nucleotide Archive (ENA) with project number: PRJEB26011. Mitochondrial phylogenies are available at https://osf.io/g5c8k/.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6397/85/suppl/DC1
Materials and Methods
Figs. S1 to S20
Tables S1 to S32
References (*26*–*187*)

11 January 2018; resubmitted 13 February 2018
Accepted 4 June 2018
10.1126/science.aas9411

Science

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Science **361** (6397), 85-88.
DOI: 10.1126/science.aas9411

How humans got their goats

Little is known regarding the location and mode of the early domestication of animals such as goats for husbandry. To investigate the history of the goat, Daly *et al.* sequenced mitochondrial and nuclear sequences from ancient specimens ranging from hundreds to thousands of years in age. Multiple wild populations contributed to the origin of modern goats during the Neolithic. Over time, one mitochondrial type spread and became dominant worldwide. However, at the whole-genome level, modern goat populations are a mix of goats from different sources and provide evidence for a multilocus process of domestication in the Near East. Furthermore, the patterns described support the idea of multiple dispersal routes out of the Fertile Crescent region by domesticated animals and their human counterparts.

Science, this issue p. 85

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.